Thesis/
Reports
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CANADA/U.S. SPRUCE BUDWORMS PROGRAM--WEST
&
CALIFORNIA AGRICULTURE EXPERIMENT STATION
DIVISION OF ENTOMOLOGY AND PARASITOLOGY

FINAL COMPREHENSIVE REPORT
PNW-82-210

Study of Factors Determining the Density and Quality of Western Budworm Populations in South-central Oregon and Northern New Mexico

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January 18, 1984

PREFACE

This is a final and comprehensive report of investigations on the factors which influence the density and quality of western budworm populations funded by the U.S. Forest Service, Pacific forest and Range Experiment Station Grant No. PNW-82-210. This report integrates and summarizes the results of field studies conducted in northern California and south-central Oregon between 1978 and 1980, and in northern New Mexico between 1980 and 1982. Prior to the 1982 field season, partial support for this work was provided through the U.S.D.A. Science and Education Administration-- Competitive Research grants # 804-15-23 and 904-15-14, U. S. Forest Service Pacific Northwest Forest and Range Experiment Station grants PNW-80-90 and PNW-81-126.

Part of the work reported here was also done under purchase order number 40-0552-2-1161 and under cooperative agreement PNW-83-307.

Support was also provided through California Agriculture Experiment Station projects 3689H and SG3862 for the duration of the study.

Previous progress reports were submitted to CANUSA-West program management on 11/30/78, 5/27/80, 9/1/81, and

11/9/82. Additional results derived from these studies were communicated to the program management at several special workshops. This information is documented in the workshop proceedings. The specific workshops were: Foliage Growth and Budworm Feeding Workshop, Dec. 1982; Budworm Survival Workshop, Jan. 1983; Budworm Adult Dispersal and Oviposition workshop, Feb. 1983; Sampling Workshop, Apr. 1983; and a Modeling Workshop, June 1983. Interim reports on PO # 40-0552-2-1191 and coop. agreement PNW-83-307 were also provided to the program. Several additional aspects of this work has been or will be published as articles in technical Journals. Appendix A is a list of these articles indicting their present status.

INTRODUCTION

Population biologists study organisms of a single or a group of closely related species which persist in time within some (often vaguely defined) region. The objective of population biology is to understand the ecological processes which affect population size and the processes which alter the character of populations. Changes in population character include evolutionary changes. These changes in the character of biological populations may be effected by changes in biotic environments and, to the extent that management alters those environments, by resource management procedures.

Opportunities afforded managers to alter biological populations are manifold. This is, in part, a consequence of policies which may be instituted over long time periods and applied over the whole or a large portion of a region occupied by any particular species. Forest resource managers, particularly in the West where rotation ages may be a century or more and one political jurisdiction may encompass areas colonized by whole populations, should be especially cognizant of these opportunities. It should also be recognized that although there are opportunities to manage forests and greatly reduce insect impacts on productivity, some management procedures may exacerbate insect effects on yield. Management strategies aimed at minimizing or eliminating pest impacts should rely on knowledge of

processes which determine pest damage potential. This knowledge is obtained from population biology studies of the organisms concerned.

OBJECTIVES AND APPROACH

Our studies were designed to investigate the population biology of the western spruce budworm and identify processes which may be responsible for changing population density and quality. Ideally, such studies should be conducted in several strategicly located sites for many years (Clark and others 1967, pp 175-177). However, because time and resources were limited, we adopted an approach of developing life tables for populations at different locations with the hope of finding them in different phases of their gradation. An attempt was made to estimate population densities at successive stages of the life cycle for at least two generations in populations differing widely in densities. To accomplish this, three populations were selected in each of two geographic regions. One was in south-central Oregon, a region in which budworm populations were historically low (Dolph 1980), and the other was in northern New Mexico where populations were increasing to or remaining at outbreak levels.

At each site thus selected a 50 x 100 m plot was established and all trees, 5 cm DBH or larger within its boundaries were listed. For any one generation, life table

entries were obtained by sampling whole branches from 20 randomly selected host trees to obtain insect densities at five successive stages in the insects' life history. In addition, observations were made on certain qualitative characteristics which were thought to influence population performance. These studies included detailed rearings and morphological descriptions of field collected individuals, controlled matings of field collected individuals to assess the fecundity and fertility of females, studies on the rate of insect development at controlled temperatures, studies on host associations of the different phenotypes in populations, and the role of pheromones in structuring populations where different color morphs occurred. Where defoliation occurred, an effort was made to establish a relationship between population density and damage to buds and shoots. Some effort was also made to evaluate the sources of budworm mortality in successive life stages. Ultimately these supplemental studies could be integrated with life table studies to evaluate the influence of the genetic structure of populations on their dynamics. Extensive observations on the intra- and inter-tree distribution of insects were made to describe their pattern of resource utilization. Studies of insect distribution also provide some insight on how western budworm populations may be sampled efficiently under the range of conditions encountered.

Overall, we accumulated observations to complete seven life tables and parts of an additional five (Table 1).

Given this rather limited data base, analyses of relationships among life table parameters such as population trend, mortality rates, and density were limited to non-parametric statistical procedures. The appeal of this approach was that only a limited set of assumptions needed to be made about the estimates used in analysis. Specifically, the only assumptions made about the variables among which associations were sought was that they could be ranked. Inferences based on such procedures are conservative and provide information on the basic structure of the system. This analytical approach does not provide estimates of parameters for any simulation model, although the data themselves may be explored, post hoc, for estimates to be used in model calibration.

STUDY POPULATIONS

Populations selected for study in Oregon were low, causing no visible defoliation, and composed of two different larval phenotypes. These two phenotypes were thought to represent two distinct species Choristoneura occidentalis Freeman and C. retiniana (Walsingham) (=viridis Freeman) (Freeman 1967, Powell 1980, Stehr 1967). Some uncertainty about the taxonomic relationships between these species was suspected, however (Carolin 1965, Powell 1980). Our preliminary surveys of these populations revealed considerable phenotypic variation; in addition to green larval morphs, typical of C. retiniana, and brown larval morphs, typical of

C. occidentalis, larvae of intermediate coloration were found. Previous to these studies it was thought that C. retiniana was restricted to true firs (Stehr 1967) and C. occidentalis fed on both Douglas-fir and fir. Stand composition and location were therefore among the principal criteria used in study site selection. The three plots finally selected were: one on Mt. Ashland, in the Siskiyou Mountains, within the range of Douglas-fir but composed principally of white fir; one at Dry Lakes Flat on Chiloquin Ridge, east of the Cascade Range, composed of both Douglas-fir and white fir; and one on Riverbed Butte, in the Gearhart Mountains, composed of white fir and approximately 50 km east of the nearest Douglas-fir stand.

Populations in the New Mexico plots were low to high, causing noticeable to severe defoliation, and composed of larvae showing little obvious color variation. The criteria used to select plots in this region were stand composition and budworm density. Three sites were selected for study. The site on San Antonio Ridge was in a mixed conifer stand with white fir, Douglas-fir and Engelmann spruce as budworm hosts. Budworm populations had caused a trace of defoliation the previous year (1979), and were apparently rising in density. The site in Peralta Canyon was also in a mixed conifer stand, but white fir was the principal tree component of the study plot and budworm caused defoliation was moderate the previous year. The site in La Jara Canyon consisted mainly of Douglas-fir but budworm population were

chronically high.

POPULATION DYNAMICS

Life Table Studies

Four stages in each generation were sampled to obtain population densities. By plotting these densities over time, a survivorship curve was approximated. Stages selected for sampling were (1) eggs; (2) early instars mining needles and buds when feeding sites were being established, (3) intermediate sized fourth and fifth instars in expanding shoots, and (4) sixth instars and early pupae in fully expanded shoots. Estimates of adult density and adult sex ratio of the parental generation were also obtained in the New Mexico populations. Sex ratios in the sparse Oregon populations were determined from supplementary collections made late in the larval period and early in the pupal period.

The mean density of eggs per square meter of foliage in the study plots ranged through almost five orders of magnitude (Figs. 1, 2). This spans the entire range of budworm densities observed in North America. Indeed, at the lower densities, in Oregon, populations were barely detectable at 0.87 eggs per sq. m of foliage. Yet even at these densities, it was possible to sample populations at successive stages to obtain population trajectories. The trajectories obtained are similar to those obtained at higher densities

(Figs. 1,2). This should help dispel the notion (engendered by the belief that parametric statistical methods are required for analysis) that it is impossible to study populations at these extremely low densities. Omitted from figures 1 and 2 are the population estimates obtained by sampling the early instars mining needles and buds. Had they been included, there would have been an apparent increase in the population following this sample. This is an artifact of sample timing which was detected in both dense and sparse populations (see below).

There is a common general shape to the survivorship curves obtained. The greatest decline in density occurred over winter between the egg stage and when the insects began feeding on expanding shoots. Most of this mortality is thought to occur at the beginning of the feeding stage when larvae experience difficulty in establishing mines in buds or needles (Campbell 1984 Sec. 6.4.2). Because the mortality in this period is so great, varying from 59 to 99 percent (Table 1), drastic changes in this rate can have a profound influence on population trend. In one New Mexico plot, which experienced population increases, this rate was below 70 percent, whereas where populations were relatively stable this rate was above 90 percent.

The apparent increase in density observed following spring emergence could be due to several processes. It could be due to spring immigration of small larvae into the

stand. This seemed unlikely since the increase in density was experienced in all sites in all years. The second possibility is that a portion of the population could spend a second winter in diapause as larvae and emerge late as fourth instars to augment the population. This is an extremely rare occurrence in laboratory rearings and is not thought to be common in the populations studied. A third possibility is that intra-stand dispersal of small larvae may result in a net increase in density in our sample trees. The consistency of the phenomenon suggests that this is unlikely. A fourth possibility is that the emergence period of overwintering larvae from hibernacula is protracted in time. Early samples only included individuals which emerged up to the time of collection and failed to account for the individuals which emerged subsequently. Our studies showed that parasitized individuals were generally smaller than the healthy larvae in early samples and their development is known to be retarded (McGugan 1955, Lewis 1960). There is substantial evidence to support this possibility though experimental verification is necessary.

During the larval period individuals are killed by parasitoids. The most prominent species of these parasitoids, both in low and outbreak populations, attack budworm larvae before they overwinter. Hosts in which parasitoid larvae develop are killed when the unparasitized individuals are in the fourth to sixth instars. A second group of parasitoids attack small larvae early in the spring; also

killing the hosts during the fourth to sixth instars. One effect of larval parasitoids on their hosts is to stunt their growth. The result is that parasitized individuals appear (based on head capsule measurements) to be a whole instar behind the healthy population in their development. In sparse populations these parasitoids account for a substantial portion of larval mortality.

Upon pupation, the insect becomes immobile and is subject to mortality from parasitism and insect and avian predation (Campbell and Torgersen 1982, and below). A substantial proportion of mortality at this stage is also due to cannibalism of pupae by other budworm larvae. Apparent mortality at this stage varies from 56 to 87 percent. In contrast, mortality in the larval stage varies from 14 to 79 percent. On reaching the adult stage, the cohort which entered the generation has already experienced between 89.6 and 99.7 percent mortality. Mortality experienced by the adult population can not be estimated because there are no techniques available for directly estimating adult densities. Nevertheless, indirect techniques, of uncertain accuracy, are available to complete the life table.

Before the life table is completed, attempts are made to account for changes in population productivity. Thus, adult sex ratio and fecundity of females are assessed. Because eggs are only produced by females and the normal sex ratio of budworm populations is 50 percent male: 50

percent female, any departure from this ratio will effect a change in the egg laying potential of the population. In half the generations sampled, the estimated sex ratio was skewed in favor of females which was reflected in a "negative decline" in population density. In these cases sex ratio effects would compensate, to some extent, any mortality experienced earlier in the generation.

The second adjustment for population quality is a reduction in apparent survival due to the departure of mean population fecundity from the maximum observed among individuals from each plot. This integrates all effects due to starvation, sublethal effects induced by less than favorable environments, and other inimical effects which are difficult to quantify directly but are reflected by reduction in fecundity. This effect is equivalent to an apparent mortality of "normal" females which ranged from 19.2 percent to 69.9 percent.

The life table is completed by comparing the expected number of eggs produced by surviving "normal" females with the egg population actually deposited. Any discrepancy detected at this stage can be variously interpreted; losses include both premature female mortality and losses due to net emigration, while increases are attributed to net immigration; though this masks premature female mortality which certainly always occurs. These discrepancies were observed to range from an apparent (-122.7) to 77 percent reduction

in the "normal" female population.

The unsatisfactory procedures used to "close" the life table can introduce serious problems in our interpretation of population performance, particularly in sparse populations where genetic changes can easily be effected by migration. For the purposes of population dynamics, this technique is less than adequate because the importance of adult mortality relative to migration cannot be assessed.

Relative Importance of Mortality by Stage

There are two aspects of mortality and survival which are of interest in evaluating population change: the overall level of mortality which static populations face within a generation, and the variability in these rates among generations. For every species, there is a theoretical survival rate that results in a completely stable population level, ie. whose population trend is 1.0. For the budworm this that the 'mean' generation survival rate would be 0.68 percent if we assume the mean sex ratio was 50:50 male:female, females mated only once, and each laid 300 eggs, on average. This survival rate reflects the fact that only 2 adults need survive to replace 300 eggs which started the generation. Under these conditions no adjustment would be needed to close the life table, since we assume that there would be no net migration.

For example, despite a greater than one hundred-fold

difference in the initial density of the two stable populations in our study (Table 2) the mortality rates within their life tables were quite similar. The last column of each table indicates that mortality in the egg to small larvae interval was 90 percent, in the subsequent larval interval, mortality in in terms of the initial cohort approximated 3 percent, and pupae were reduced between 1.1 and 3.0 percent in the respective populations. However, there are striking differences in the effect of sex ratio and depression in fecundity in these two populations. The sparse populations experienced an increase in the proportion females, while less than half the individuals were female in the dense populations. The reduction in fecundity was only 0.1 percent in the sparse population but was six times this rate in the dense population. Thus, it was not until qualitative differences among individuals and differences in pupal survival were accounted for that significant differences were noted in stable populations in these two density ranges.

The other important aspect of mortality is the pattern in which mortality rates in the different age intervals vary within generations. Theoretically, mortality within an age interval which varies closely with variation in generation trend is considered to have a major effect in determining that trend. To get an adequate sample of life tables for a given location, which would allow an adequate display of this variation and a calculation of the degree to which

variation in trend depended on variation in mortality rates within any one interval, requires time and resources beyond those available in short term projects of this sort. As a compromise, one may examine fewer life tables of populations in several locations, hope that the spectrum of situations sampled spans the range of conditions experienced by the species under study, and then rely on faith that the results reflect the behavior of the system studied. A major flaw in this approach is that time lags in the effect of any process, suspected to affect trend in some budworm populations (Royama 1977), could not be detected using this method. This approach therefore limits the investigator to detecting first order effects only; i.e. only processes whose actions occur and whose effects on population trend are experienced in the generation studied can be evaluated. Furthermore, since the dynamics of populations differ and their performance may depend on the physiographic and biotic provinces in which they evolved, comparisons of the sort attempted here confound differences associated with density with all the variables associated with differences in location. Populations in Oregon appear to be composed of two partially isolated species (see below) and together they differ from the populations in New Mexico. Therefore, only the broadest generalizations are possible with the results obtained.

With these disclaimers clearly in mind, the Spearman rank correlation coefficients between population trend and survival rates within the different periods of the

generation sampled were determined. Use was made of data from the seven complete life tables displayed in Table 1. Both survival of larvae from establishment in their feeding sites to pupation and survival from pupation to adults were statistically correlated with population trend (Table 3). The Spearman rank correlation coefficients between pairs of the life table entries were examined to detect any structure in the functioning of the population systems. High larval survival was negatively correlated with the proportion of females in the population as in the dense increasing populations in New Mexico. The sparse, Oregon populations which experienced low trends also experience low survival rates among larvae and their sex ratios were shifted in favor of females. The terminal life table adjustment, used in closing the life table, was also positively correlated with both high mortality in the larval stage and the proportion of males in the population. In sparse populations, especially, there is an associated reduction in the number of eggs observed from that expected, despite the compensatory effects of the sex ratio shift favoring females and offsetting high pupal mortality.

These observation suggest that mortality in no single life stage dominates the budworm life system to influence trends in natural populations. Rather, survival in both the larval and pupal stage combine to determine trend. Mortality rates in the period from eggs to the feeding stage is a large component of the overall generation mortality in

stable populations. Though not significantly correlated with population trend in this study, under certain conditions, survivorship in this period could increase dramatically to change populations from a sparse phase to the outbreak phase.

The correlations obtained suggest what life stages should be investigated to find mechanisms responsible for population change. However, to be effective in regulating population density (driving them back to equilibrium) requires that the mortality rate increases with increases in density (i.e. it is density dependent). Mortality which is negatively correlated with density (negatively density dependent) tend to destabilize populations. In both cases, the degree to which these mortality rates affect population trend depends upon the degree to which they respond to changes in population density. Without having recourse to experimental manipulations of the system we have to rely on correlations to assess this dependence.

Larval mortality rates and fecundity reduction are not significantly associated with density, but mortality rates from egg to establishment of the larvae feeding on shoots and the sex ratio effect are positively correlated with density and pupal mortality is negatively correlated with density (Table 4).

The mortality from eggs to the establishment of larvae appears to be density dependent at both the density ranges

studied (Fig. 3). The two distinct cluster of points represent the populations in each of the two density ranges. Coincidentally the single point which appears to be an outlier represents the case where the population trend was 8.36, the largest trend recorded. This strongly suggests that where the rate of population increase is large--the transition from sparse to dense populations--high survival rates at this stage of the life cycle are involved. Within populations which are more stable, these mortality rates appear to be strictly density dependent and regulatory in nature.

Mortality rates of large larvae and pupae may be density dependent at the extremely high population densities but largely density independent at the low densities (Fig. 4). However,the degree of density dependence is low because the slope of the line at the high densities does not appear very large. Thus the regulating effects of this negative density dependent mortality may not be very strong in these populations.

The sex ratio effect appears to be density associated only at the lower density limits (Fig. 5) and may play a major role in regulating populations at the lower extremes of density.

The rather surprising observation that fecundity reduction has no overall association with density is, in part, a result of a lack of any effect at low population densities.

There appears to be a positive density association at high densities (Fig. 6). It is likely that the apparent density dependence of fecundity reduction at higher densities is caused by the effect of increased defoliation resulting in food deprivation which ultimately reduces fecundity. At low densities this stress did not occur.

The overall significance of these results is that they give some indication of how the life system functions but more importantly they suggest areas where further research would be warranted and where control tactics used in different management strategies would be most likely to be effective (see below).

Processes Affecting Post-diapause Survival Rates

As noted above, survival from eggs to actively feeding larvae, from the end of the sixth instar through the pupal stage to adult emergence, and the effects of sex ratio variation are all statistically correlated with budworm density. Survival from eggs to actively feeding larvae is also influenced by several other factors (Campbell 1984 6.4.2) among which is the degree to which budworm emergence from hibernacula is synchronized with host phenology. The relationship between host tree development and the characteristics of insect emergence in spring are dealt with below.

Attempts were made to determine what processes influenced pupal survival by monitoring the fate of approximately

270 naturally occurring tagged pupae in one stand in 1981 and in each of two stands in 1982 under high budworm population densities. Whereas pupal survival was highest in lower crowns and in trees growing in the open or at the forest edge in 1981, no such differences were detected in 1982. In 1981, the greatest sources of mortality at this stage were insect parasites and predation by other insects (Table 5). Cannibalism by budworm larvae which had not yet pupated was included in this category. Pupae that died of unknown causes accounted for an intermediate proportion of mortality in 1981. Pupae that were missing, presumably preyed upon by birds, ants, and other insects which remove whole insects, accounted for the lowest proportion of the observed mortality in 1981, but appeared higher in both plots in 1982. The relative importance of parasites remained the same over all plots in 1982. However, at Peralta Canyon, predation by other insects decreased to less than half its value in the previous year, while the proportion of insects which were missing increased by approximately half again. Over the 2 years and in both plots in 1982, the combined effects of predation by other insects and agents which remove whole pupae from the branch remained remarkably constant. It would appear that the number of pupae which disappear is relatively constant; thus the proportion would be inversely density related. However, predation by insects varies in the opposite way, becoming more intense with the higher budworm densities, possibly reflecting the effects of

crowding and an increased incidence of cannibalism.

In comparing the survival rates estimated from tagged pupae with those derived from life table plots for the interval spanning late sixth instar to adult emergence, it is evident that there is substantial mortality in the period during which larvae transform to pupae. Survivorship curves obtained from the tagging studies indicate that prepupae and early pupae suffer much greater mortality than fully developed pupae. Another large source of mortality occurs toward the end of the pupal stage when most pupal parasites emerge from their host. Over the range of densities studied, the percentage mortality due to parasitism remained constant.

The role of parasitoids that affect the larval stages is quite different. Although mortality in the larval stages is not correlated with generation survival, this mortality can be quite high in stable populations, be they sparse or dense. In some cases, parasites as a group may account for all the observed mortality of large larvae estimated from life tables in both dense and sparse populations. Thus it is likely that they can function in setting the general equilibrium levels in stable, sparse populations. The interaction with other contemporaneous sources of mortality will mask their potential (Morris 1958) and the effects of individual parasitoid species are difficult to evaluate because the characteristics of interspecific competition are

not fully known (Royama 1981).

The parasite fauna of the sparse and dense populations differ. Whereas Glypta fumiferanae (Vier.) and Apanteles fumiferanae Vier. are common budworm parasites throughout North America (Campbell 1984 sec. 6.6.2.1), G. fumiferanae is virtually absent from sparse populations. Dolichogenidea (new species) and the Campoplegine Ichneumonid wasps assume a more important role in sparse populations where G. fumiferanae is rare. By contrast, G. fumiferanae is often the second most common parasite, after Apanteles spp., recovered from dense populations.

The significance of this difference is difficult to evaluate since the life history of Dolichogenidea n.sp. is not known. Because the larvae parasitized by either G. fumiferanae and A. fumiferanae are retarded (McGugan 1955, Lewis 1960) and these parasitoids overwinter in overwintering larvae, losses of unparasitized larvae due to asynchrony with host development (see below) would tend to increase the apparent killing power of these parasites for a given oviposition effort. Such a large increase in effective parasitism would not be realized by the Campoplegine Ichneumonid parasites since our records suggest they parasitized hosts in the Spring. More detailed studies are required to evaluate the significance of these life history differences to the success of host populations.

How distorted sex ratios in sparse populations are produced is not understood. There is the possibility that parasitoids may influence sex ratios by selectively parasitizing males but there is no direct evidence for this in larval budworm populations. Cannibalism in the early pupal stages which would favor females (since they pupate after males) is unlikely to account for the effect observed in sparse populations because interspecific encounters would be rare at these densities.

Spatial Distribution of Insects

The distribution of insects within the forest varies among stages, seasons, and locations (Waters and others 1984). It thus appears that the outcome of mechanisms which determine the distribution of a particular stage depends on the distribution of insects in previous stages. Consequently, the peculiar distribution observed in a stand at a particular stage may be unique to that stand and season. Insect density also affects the characteristic distribution of insects within a stand. At low densities, the insects appear to occur independently of one another, whereas at higher densities, there appears to be considerable aggregation, and at extremely high densities, when almost all available resting sites are occupied, the distribution becomes more uniform (Waters and others 1984).

Observed insect distributions are a result of the counteracting mechanisms of aggregation and dispersal together

with the effects of any anisotropic mortality. In addition, the mobility of feeding larvae and adults further complicates descriptions of insect distribution. Despite these difficulties, it appears that there are significant differences among crown strata within trees and among trees. The biological processes which account for these differences are presently unknown.

Because budworm distributions are so labile, and because spatial and temporal variation is so large, any sampling procedure that requires counting insects on foliage to obtain data for estimating density must deal with these complications explicitly. Procedures must be designed to include sample units from each crown level from host trees of all size classes. Ideally, sample units, selected with known probability, should be allocated in a manner that reflects the distribution of foliage within stands. Techniques exist which allocate sample units to achieve a given level of precision with minimum cost. However, random sample unit selection coupled with the size of western trees growing in inaccessible stands may render such procedures prohibitively expensive. Yet, to relax any of these requirements renders such density estimates almost worthless in making statistically sound inferences. Such techniques are probably inappropriate for certain types of monitoring in the West. Alternative, less costly, techniques should be sought.

INDIVIDUAL VARIATION AND POPULATION PERFORMANCE

The preceding demographic analysis ignored most qualitative characteristics of individuals. Collectively, individual qualitative characteristics determine population potential. These qualitative characteristics are not of equal value in determining population performance, however. Variation in many of the characters studied must be considered explicitly in the design of pest-management procedures such as monitoring, control treatments, and post-treatment evaluation surveys.

Of prime importance to both the pest manager and the population biologist is an understanding of relationships between the target population and any related populations in the habitat under study. The sympatric occurrence of C. occidentalis and C. retiniana in south-central Oregon creates problems for pest managers contemplating the use of species-specific or monitoring control techniques. The identification and taxonomic status of budworms feeding on Douglas-fir and true firs in this region is confusing (Carolin, chapter 3; Powell 1980, Volney and others 1984). Stehr (1967) noted that Douglas-fir was the principal host of the western spruce budworm (C. occidentalis) but the 'Modoc budworm' (C. retiniana) only occurred on true firs. Nevertheless, where the ranges of the two species overlapped, there was little doubt that the two species would come into contact, because the western budworm also fed on

true firs. Harvey and Stehr (1967) used larval and pupal coloration while Freeman (1967) suggested that adult coloration may be used in distinguishing the two budworm species. Larvae of the western spruce budworm are predominantly brown in the sixth instar whereas larvae of the Modoc budworm are almost entirely green. Field and laboratory studies indicated, however, that there is considerable color variation in the sympatric budworm populations of mixed Douglas-fir/white fir stands in south-central Oregon (Volney and others 1984a).

Color Variation

Progeny from field collected parents of known larval color were reared under controlled conditions to elucidate the manner in which coloration is determined. In general, matings in which both parents were green larvae produced progeny in which all larvae were green. Almost 100 percent of the offspring from parents that were brown larvae also became brown larvae. Crosses between the two morphs produced about 64 percent brown larvae, 25 percent intermediate larvae, and 10 percent green larvae. A small proportion of green and intermediate larvae occurred in a single anomalous family from a mating of brown parents. It was thought that one or both parents in this mating were derived from hybrid natural matings (Volney and others 1984). It was shown, further, that the frequency of morphs in families containing intermediate individuals was dependent on the

rearing temperature. At low temperatures (15¢there was a higher proportion of heavily pigmented (brown) individuals than at the higher rearing temperature (25¢and tended to be darker than females (Volney and others 1983b). Color differences associated with moths of the different larval types are not absolute; thus the identification of an individual as belonging to one or other of the species was impossible in these populations. There was, nevertheless, an association between larval coloration and adult forewing coloration (Volney and others 1983b). Brown larvae, typical of C. occidentalis, tended to become reddish brown moths with prominent forewing bands, but green larvae, typical of C. retiniana, tended to become greyish brown moths with indistinct forewing bands.

Correlated with larval color is substantial variation in certain qualitative characteristics that are important in determining population success. These characters include host associations, developmental rates, and fecundity. In each case, the extent to which variation in larval coloration is associated with variation in the particular trait was been determined.

Host Associations

The occurrence of the different larval morphs on the various host species is similar to that described by Stehr (1967) except that C. retiniana (green larvae) were found feeding on Douglas-fir in addition to its principal host:

white fir. Within any mixed Douglas-fir/white fir stand the different larval color morphs were not faithful to their respective principal hosts. Rather, the frequency of the different morphs within a stand was strongly associated with the relative basal areas of Douglas-fir and white fir (Fig. 7, Table 6).

Ecological separation, mediated by these host associations, does not appear to be an effective barrier preventing the two morphs from occurring on the same tree species in nature. The preponderance of brown larvae on Douglas-fir and green morphs on white fir (Table 6) probably indicates differential survival rates of the two morphs on the two host species rather than any oviposition preference. Fall and spring dispersal can result in substantial redistribution of larvae within stands (Beckwith and Burnell 1982). At low densities this may result in a rather even distribution of larvae with respect to host foliage in the stand and would tend to counter any any host associations resulting from oviposition preferences. Each morph is camouflaged by its coloration if it feeds on a shoot of the appropriate host. However, these differences in coloration only become evident in the later instars and pupae, after dispersal has occurred. Any differential mortality of morphs on the wrong host, induced by avian predation for instance, is constantly counteracted by passive dispersal of larvae. The magnitude of this differential mortality has not been incorporated in life tables to date but the net effect would be to reduce

survival of both budworm populations relative to populations of a single species in stands with only one host.

Foliage resource depletion did not influence the success of sparse populations. Where populations are high, such as in the New Mexico plots, the relationship between defoliation and insect population intensity, which may determine starvation rates and dispersal loss, depends on the host species fed on. It is apparent that Douglas-fir can sustain much higher budworm densities than white fir. Fig. 8 shows that to achieve a certain degree of defoliation, much higher population intensities are required on Douglas-fir than on white fir. This difference is partly due to the peculiar reaction of each species to repeated budworm feeding. Heavy feeding on Douglas-fir apparently induces latent buds, produced in previous years, to flush and expand as shoots, whereas, few if any such buds are activated on white fir. On most Douglas-fir shoots, the number of latent buds exceed the number vegetative buds produced (Volney 1984) and thus endow these trees with a resilience to defoliation not evident in white fir. A consequence of this is that populations may persist at high levels for longer periods on Douglas-fir than on white fir before tree mortality becomes apparent. Figure 8 shows that the population of white fir buds declined substantially during the period of budworm feeding whereas the number of Douglas-fir buds did not, even though the Douglas-fir stand had sustained much higher budworm populations than the white

fir stand. It is therefore reasonable to expect that Douglas-fir stands can sustain outbreaks for longer periods than similar stands of white fir.

A consequence of Douglas-fir resilience to budworm feeding is that the proportion of brown larval morphs in the population will tend to increase as this feeding continues. The decline in the proportion of white fir shoots in the stand and the resulting reduced survival of green larval morphs feeding on Douglas-fir will favor brown morphs.

Changes in the population to favor brown larvae are likely to result from two additional processes. Any natural matings between the two species in South-Central Oregon will result in an approximately 90% of the offspring being brown or intermediate in coloration. Although such matings are infrequent, they do occur in nature (Liebhold and others 1984, Volney and others 1984a). Further, the fecundity of brown females is half as large again as their green counterparts in any one stand (Volney and others 1984a), further contributing to the preponderance of brown larvae in mixed stands.

Variation in Spring Emergence

The period over which larvae emerge from hibernacula in the spring is quite variable (Volney and others 1983a). Since survival at this stage is thought to be important in the dynamics of budworm populations (Campbell 1984 Sec

6.4.5) the process of emergence from hibernacula in relation to host tree phenology could play a major role in determining the success of insects in establishing feeding sites. Insects which emerge early must mine needles before the buds have swollen sufficiently to permit bud mining. There is considerable variability in the proportions of budworm larvae mining needles, mining buds, or wandering free on sample branches in the early spring collections (Fig. 10). Needle mining and wandering to locate buds in a suitable state of development exposes budworm larvae to increased mortality due to needle fall, dispersal, and predation. Similarly, in dense populations, insects which emerge late may find it difficult to find live buds, buds in a suitable state of phenological development, or to colonize buds occupied by more advanced larvae, thus being forced to wander and also risk mortality. The period over which the progeny of a single female emerge in the spring may be protracted. This would tend to ensure that some portion of each family will survive regardless of host phenology (Volney and others 1983a). Also, the pattern of emergence among families is very similar; most individuals leave hibernacula early. The effect of these skewed emergence distributions is that widely different survival rates can result depending on when bud break occurs. Also, any process which extends the length of the phenological window during which feeding sites may be established, if appropriately timed, could increase survival dramatically.

The pattern of emergence from hibernacula also differs between larval color morphs (Volney and others 1984b). Larvae which became green in later instars emerged before their brown counterparts. Progeny from interspecific matings become active at periods intermediate between these two extremes. Preliminary analyses of host phenology indicate that white fir buds usually break slightly before those of Douglas-fir. It would therefore appear that emergence of larvae which become green in the later instars would be synchronized better with white fir bud development and their brown counterparts with that of Douglas-fir.

Reproductive Isolation

If survival of each species varies under different conditions and is attributable to possessing a constellation of differentially adaptive characters, then the mechanisms which maintain the genetic integrity of each species are important in preventing the break up of character combinations where the two species are sympatric. In sympatric populations, the frequency with which the isolating mechanisms break down would play a major role in determining the success of the two species. The budworm populations in mixed white fir/Douglas-fir stands of south-central Oregon are faced with this situation. Understanding the nature of isolating mechanisms which preserve the genetic differences between the two species could provide a new means of manipulating the densities of these populations.

There is no evidence that any post-mating isolating mechanisms are effective in preventing hybridization. Crosses between the two species are easily obtained in the laboratory and there in no evidence of reduced viability of the offspring (Volney and others 1984a).

The relative development of the two species changes as they grow. By the end of the fifth instar, the development of brown morphs is sufficiently more rapid than that of green morphs to compensate for the difference in emergence from hibernacula. As a result, both morphs enter the sixth instar simultaneously. Also, durations of the sixth instar and pupal stage do not differ between the species.

The synchronous occurrence of large larvae, pupae and moths of both species in the field implies that these stages are subjected to the same array of natural enemies. Any differential survival of the two types of insects during this time must be due, in part, to the differences in distribution of the insects with respect to host species and the relative efficiencies of natural enemies in killing each type of insect on each host tree species. However, these agents are not 100 percent effective in reducing the populations of the respective species on the secondary hosts. Thus, ecological isolation, mediated by host factors, does not isolate the species.

Several aspects of the pre-mating behavior are not sufficiently different to prevent inter specific crosses in

nature. A consequence of the similarity in developmental rates is that moths of both species fly at the same time in any one season (Volney and others 1984b). Further, there is considerable overlap in the time of day as well as the season that moths are sexually active in the field (Liebhold and Volney 1984a). Since both species are sexually active simultaneously, temporal differences are not responsible for maintaining the genetic integrity of each population.

Males of each species are attracted to synthetic attractants in both host and non-host tree species, further indicating that host species specific factors play a minor role in maintaining reproductive isolation between the two species (Liebhold and Volney 1983). There is no evidence that close range mating behavior of either sex prevents inter-specific matings (Liebhold and Volney unpub. data.).

To date, the composition of pheromones released by females and perceived by males as an attractant is the only factor known to isolate the species reproductively (Liebhold and others 1983, Sanders and others 1977). However, there is evidence that even this isolating mechanism is less than perfect in the mixed populations of south-central Oregon (Liebhold and Volney 1984a). The occurrence of intermediate larvae in nature, the occurrence of females with intermediate pheromone specificity, and individuals which produce mixed families in test crosses are evidence that hybridization occurs in the field (Liebhold and others 1984, Volney

and others 1984a). Experiments with virgin females have also revealed that the behavior of hybrid females in attracting wild males would promote interspecific genetic exchange. The frequency of wild interspecific matings in this area is not as yet known. It would appear that such crosses occur sufficiently often, however, to offset the development of genetic incompatibilities between the species. Consequently, the populations appear to be structured such that there are two partially isolated species in which a measure of genetic exchange is maintained. Cursory observations suggest that this phenomenon is not limited to south-central Oregon but may extend north into the central Cascade Range and northeast into the Blue Mountains (Liebhold pers. comm.).

SIGNIFICANCE OF RESULTS

The results of life table studies to date have been successful in suggesting fruitful areas for future work on western spruce budworm population ecology. Perhaps most important, is the identification of early larval survival as being density associated in both sparse and dense populations and its possible importance in the transition of populations to the outbreak phase. Although the exact mechanism responsible for population release is not known, the combined effects of parasites in overwintering budworm populations, and host tree phenology relative to insect development, particularly the processes which determine emergence

from hibernacula, will figure prominently in determining the rate of population change at this critical stage of the budworm's life cycle. Once the details of the mechanism are known, it may be possible to manipulate budworm populations to maintain them at tolerable levels and prescribe long term management procedures.

Spruce budworm populations appear to be bimodal: they are stable in two distinct density ranges and make transitions rather rapidly (Jones 1977). If this is also the case for western spruce budworm populations, as suggested by our results and Campbell (1984), population suppression tactics aimed at dense populations are unlikely to succeed. The mortality that would have to be imposed on dense populations to reduce them to the sparse density range exceeds the degree possible with current direct control technologies. The stabilizing effect of density dependence in large larval mortality rates of dense populations would also tend to frustrate efforts which failed to suppress populations sufficiently while leaving the life system otherwise unchanged. It is therefore clear that management of budworm populations should be concentrated on preventing populations from becoming dense. The density at which this critical level is achieved lies somewhere between 10 and 40 eggs per square meter of foliage.

It would appear that control procedures should concentrate on reducing early larval survival. The procedure

usually recommended is to manage stands in a fashion which maximizes loss of larvae through dispersal (Campbell 1984, Sec. 6.4.2.4). Such procedures, however, presume we are able to control stand structure in an as yet unspecified manner; are labor intensive, possibly requiring repeated stand entries which might aggravate other problems such as root disease; and are costly.

Our results indicate that sex ratios in sparse populations are skewed in favor of females and fecundity reduction is correlated with sex ratio (table 3). These data also suggest that this sex ratio effect may also be inversely correlated with population trend. Thus a reduction in eggs per female will have the expected effect of reducing population trend as well, barring immigration into the population. Opportunities to exploit a system that operates in this fashion with the intent of preventing populations from erupting are also indicated by these results.

Any process which guarantees that males mate, on average, less than once is likely to achieve the desired reduction in the mean number of eggs laid per female. There is a possibility that sex attractants may be used to this end by interfering with the mating behavior of males. Such an approach would be among the least disruptive treatments possible, the most species specific imaginable, and among the safest environmentally cheapest which could be implemented.

Clearly there is a need to verify the results of these population studies over a larger geographical region, experiment with techniques to reduce the success of males in finding mates, and to determine whether reduced mating success results in the desired population reductions. Perhaps the most significant achievements of these studies to date are: recognition the possibility of preventing outbreaks by manipulating sparse populations at a specific period in its life history, and developing information which could be applied in implementing such an approach. The approach is not without problems. Selection of the proper pheromones is critical in such techniques. Studies of individual variation in female attractant specificity and the reaction of males to pheromones have been valuable in illustrating the type of variation which might be encountered. Similarly, little is known about the relationships among early larval survival, establishment of larvae on their feeding sites and the pattern of larval emergence from diapause.

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TABLE 1

Table 1. Life table statistics for populations sampled.

Plot	Generation	Initial density	Trend actual	Trend expected	Percent Reduction in Density at Successive Stages of a Generation: eggs	Larvae L-4&5	L-6 & pupae	Adults (sex ratio)	Fecundity reduction	Unaccounted mortality
SR	80-81	46.12	8.37	9.16	68.2	39.8	56.3	-2.1	22.9	8.6
SR	81-82	386.1	-	4.50	83.5	47.6	70.9	20.6	19.5	-
PC	80-81	262.9	2.96	4.14	58.9	45.0	75.0	8.0	52.4	24.9
PC	81-82	778.5	-	0.90	91.8	35.7	75.6	66.3	40.0	-
LC	80-81	1685	1.17	0.94	92.1	45.4	69.6	10.0	54.5	-17.2
LC	81-82	1849	-	0.74	99.0	42.9	77.8	22.5	29.1	-
MA	78-79	2.43	0.76	1.13	90.4	14.0	81.0	10.0	69.9	-34.0
MA	79-80	1.84	0.68	1.08	76.1	65.0	70.1	-13.0	-19.2	50.0
RB	78-79	-	-	-	-	24.2	87.1	-50.0	62.1	-122.7
RB	79-80	12.28	0.17	0.77	95.6	67.1	81.0	-30.0	31.1	77.8
DF	78-79	-	-	-	-	-	87.5	-34.0	59.7	10.0
DF	79-80	0.87	0.40	1.78	82.4	79.1	84.4	-80.0	33.3	55.0

*SR--San Antonio Ridge, PC--Peralta Canyon, LC--LaJara Canyon, New Mexico; MA--Mt. Ashland, RB--Riverbed Butte, DF--Dry Lakes Flat, Oregon.

** Eggs per sq. m.

TABLE 2

Table 2. Life table in sparse and dense populations in which trend approached 1.0

Stage x	1979/80 generation, Riverbed Butte, Oregon: Estimated population density (per sq. m) lx	Reduction in density dx	Percent density reduction in interval 100qx	Percent density reduction in generation dx/eggs	1980/81 generation La Jara Canyon New Mexico: Estinated population density (per sq. m) lx	Reduction in density dx	Percent density reduction in interval 100qx	Percent density reduction in generation dx/eggs
Eggs	12.28	11.73	95.6	95.6	1685	1552	92.1	92.1
L-4&5	0.544	0.365	67.1	3.0	132.9	60.35	45.4	3.6
L-6/pupae	0.179	0.145	81.0	1.1	72.6	50.5	69.6	3.0
Adults	0.034	-0.01	-30.0	-0.1	22.1	2.21	10.0	0.1
Females x 2	0.0438	0.0136	31.1	0.1	19.86	10.82	54.5	0.6
Normal fems. X 2	-0.302	0.0235	77.8	0.2	9.04	-1.55	-17.2	-1.1
Expected eggs	9.45				1577			
Actual eggs	2.1				1849			
Expected trend	0.77				0.94			
Actual trend	0.17				1.17			
Generation survival--	0.0025				0.0054			

TABLE 3

Table 3. Spearman's rank correlation coefficients among life table entries.

	Survival rates					
	Eggs to L-4 S_E	L-5 to pupae S_L	Pupae to adults S_P	Sex ratio effect P_f	Fecundity reduction F_f	Unaccounted mortality M
Trend (I)	0.642	0.750*	0.741	-0.652	-0.142	0.679
S_E	-	0.321	0.419	0.008	0.524	0.107
S_L		-	0.455	-0.723	-0.392	0.857*
S_P			-	-0.420	0.295	0.513
P_f				-	0.607	0.902*
F_f					-	0.607

*Coefficient significantly different from 0, alpha = 0.05.

TABLE 4

Table 4. Association of age interval mortality rates with population density.

Age interval	Spearman's rank corr. coeff.	Number of cases	t statistic
Eggs to L-4	0.745	10	3.159*
L-4 to L-6/pupae	-0.374	11	-1.275
L-6/pupae to adult	-0.703	12	-3.124*
Sex ratio effect	0.834	12	4.786*
Fecundity reduction	0.316	12	1.074

*Coefficient significantly different from 0, alpha = 0.05.

TABLE 5

Table 5. Causes of pupal mortality in dense populations.

Plot	Year	Budworm density*	Fate (%) Survived	Missing	Predation**	Parasitized	DOC***	Number monitored
Peralta Canyon	1981	59.6	62.9	6.8	11.0	10.6	8.6	264
Peralta Canyon	1982	40.9	62.8	10.2	4.6	13.3	9.1	264
San Antonio Ridge	1982	33.3	66.8	16.0	1.5	9.9	5.7	262

*Insects per sq. m foliage.

**Predation by arthropods.

Dead of unknown causes.

TABLE 6

Table 6. Relatve frequencies of morphs on white fir and Douglas-fir.

Plot name	Number of larvae in sample	% on white fir			% on Douglas-fir		
		Green	Intermediate	Brown	Green	Intermediate	Brown
Mt. Ashland	111	96.4	2.7	2.7	-	-	-
Riverbed Butte	181	100.0	0	0	-	-	-
Dry Lakes Flat	70	1.7	3.3	8.3	1.7	15.0	
Tolman Creek	100	0	1.0	15.0	3.0	72.0	
Hyatt Lake	69	2.9	1.5	0	5.8	2.9	87.0
Dutch Oven Flat	100.0	0	0	-	-	-	

FIGURE CAPTIONS

Figure 1. Trajectories of sparse budworm populations in south-central Oregon, 1979-80.

Figure 2. Trajectories of dense budworm populations in northern New Mexico, 1980-82.

Figure 3. Relationship between egg density and mortality from eggs to the fourth instar.

Figure 4. Relationship between larval density and mortality of large larvae.

Figure 5. Relationship between density of pupae and 'apparent mortality' due to sex ratio effects. A: Sparse populations. B: Dense populations.

Figure 6. Relationship between density and fecundity reduction.

Figure 7. Association between the rank of % brown larvae in stand and rank % Douglas-fir basal area in host tree component at site.

Figure 8. Regression relationship of population intensity and defoliation on Douglas-fir and white fir.

Figure 9. Response of bud populations to budworm defoliation in stands where defoliation was severe.

Figure 10. Distribution of western spruce budworm feeding

habits in dense New Mexico populations, early spring 1982.

FIGURE 1

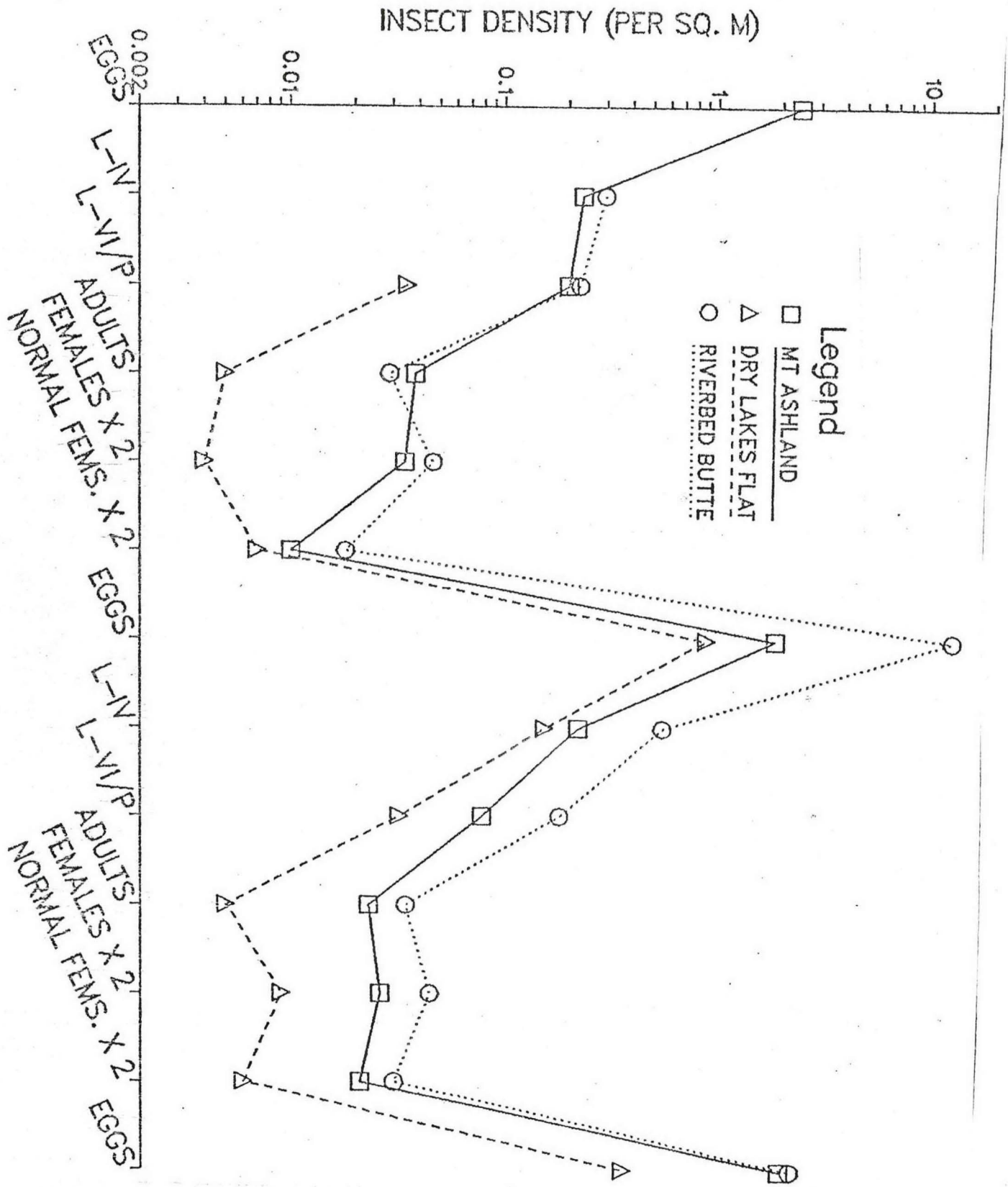

INSECT DENSITY (PER SQ. M)
0.002
0.01
0.1
1
10
EGGS
L-IV
L-VI/P
ADULTS
FEMALES X 2
NORMAL FEMS. X 2
EGGS
L-IV
L-VI/P
ADULTS
FEMALES X 2
NORMAL FEMS. X 2
EGGS
Legend
MT ASHLAND
DRY LAKES FLAT
RIVERBED BUTTE

FIGURE 2

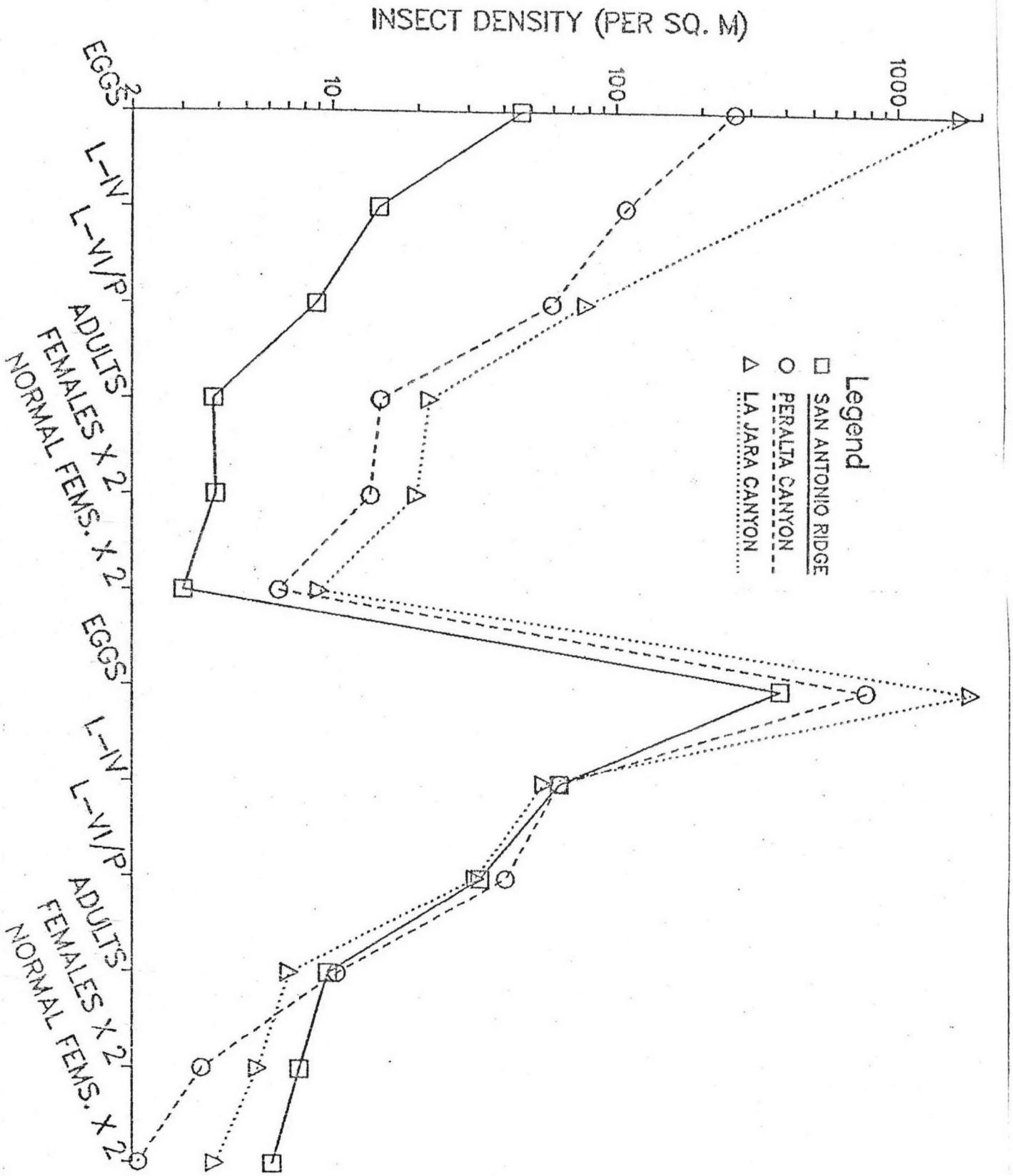

INSECT DENSITY (PER SQ. M)
1
10
100
1000
EGGS
L-IV
L-VI/P
ADULTS
FEMALES X 2
NORMAL FEMS. X 2
EGGS
L-IV
L-VI/P
ADULTS
FEMALES X 2
NORMAL FEMS. X 2
Legend
SAN ANTONIO RIDGE
PERALTA CANYON
LA JARA CANYON

FIGURE 3

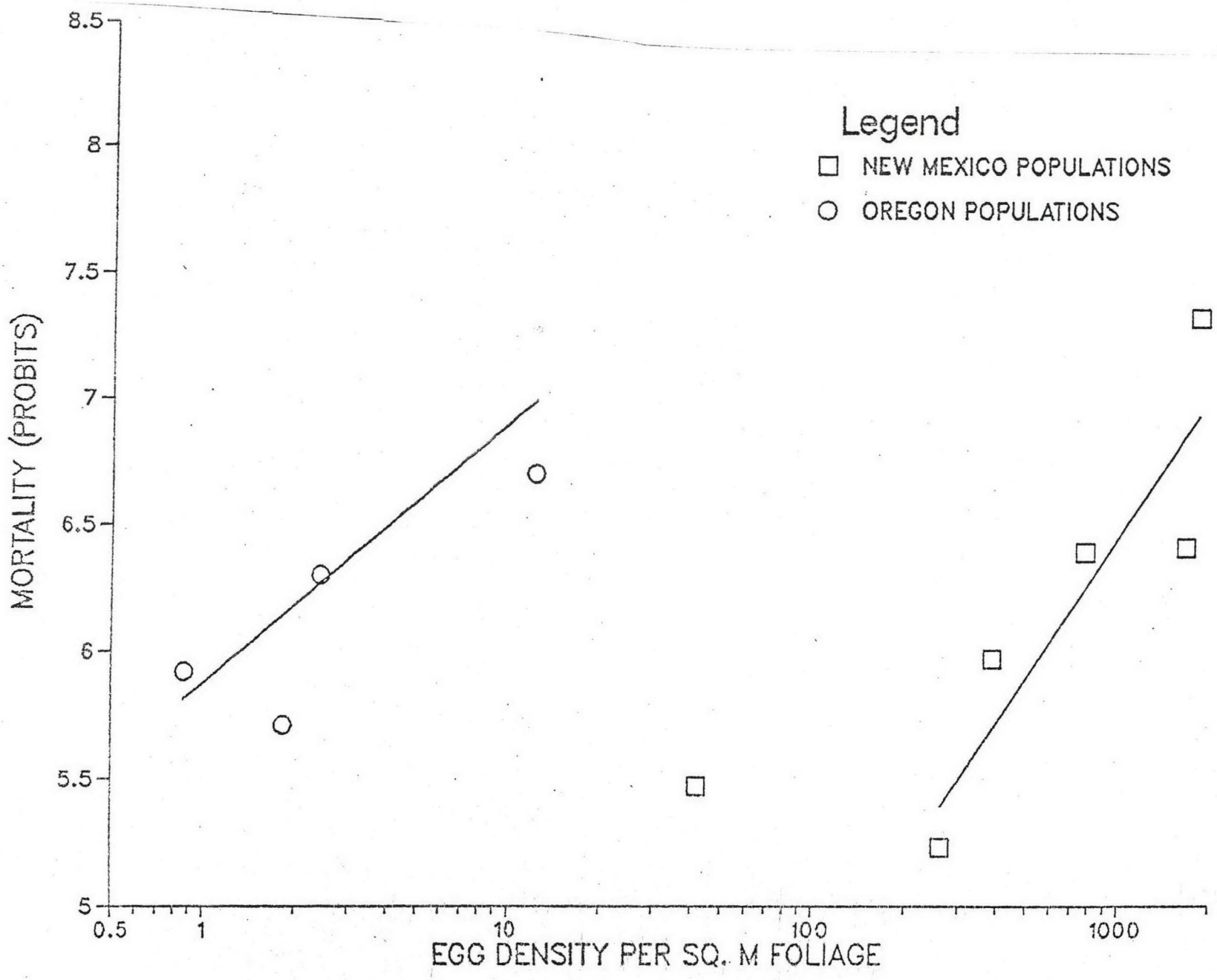

Legend
NEW MEXICO POPULATIONS
OREGON POPULATIONS
MORTALITY (PROBITS)
8.5
8
7.5
7
6.5
6
5.5
5
0.5
1
10
100
1000
EGG DENSITY PER SQ. M FOLIAGE

FIGURE 4

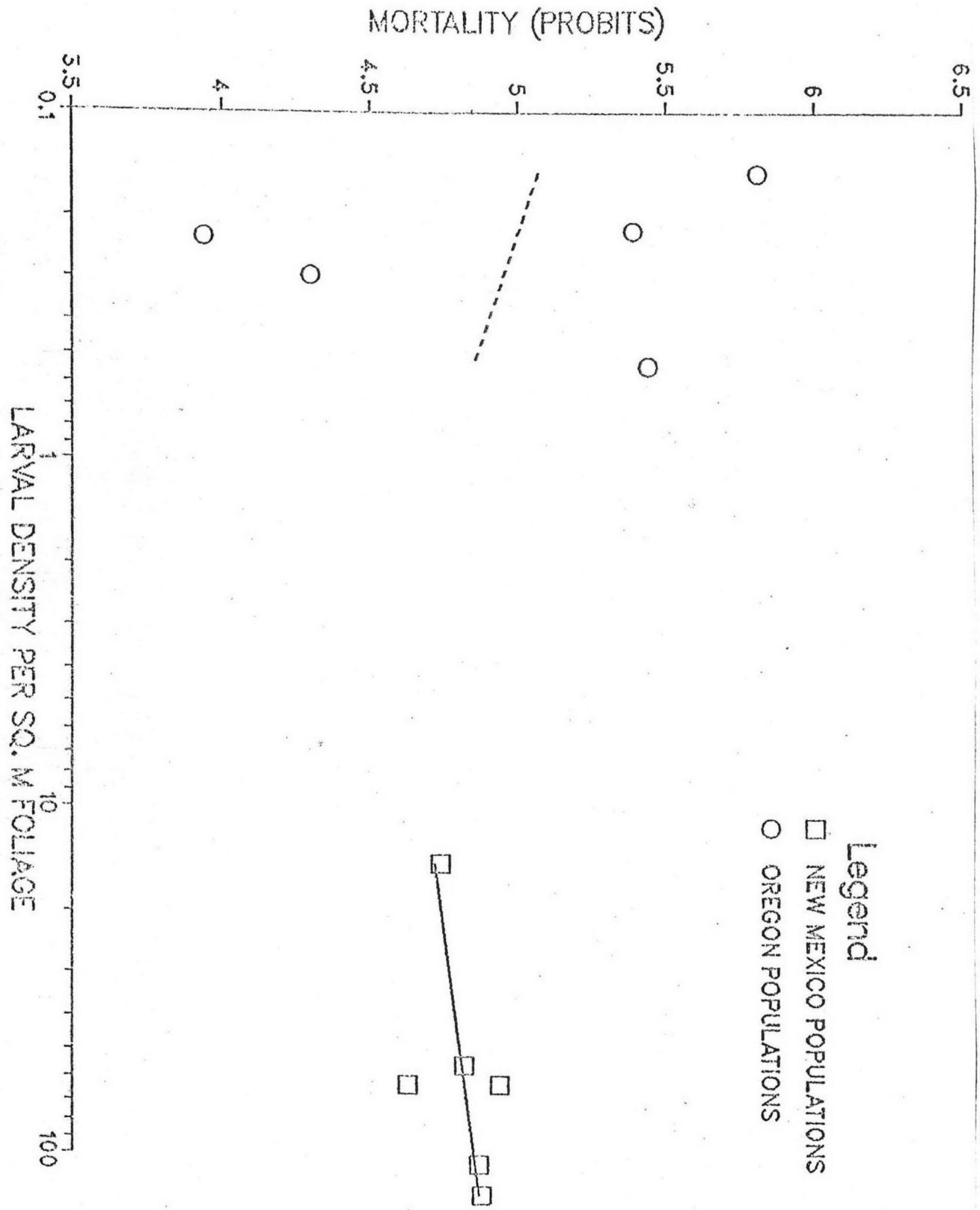

MORTALITY (PROBITS)
5.5
4
4.5
5
5.5
6
6.5
0.1
1
10
100
LARVAL DENSITY PER SQ. M FOLIAGE
Legend
NEW MEXICO POPULATIONS
OREGON POPULATIONS

FIGURE 5

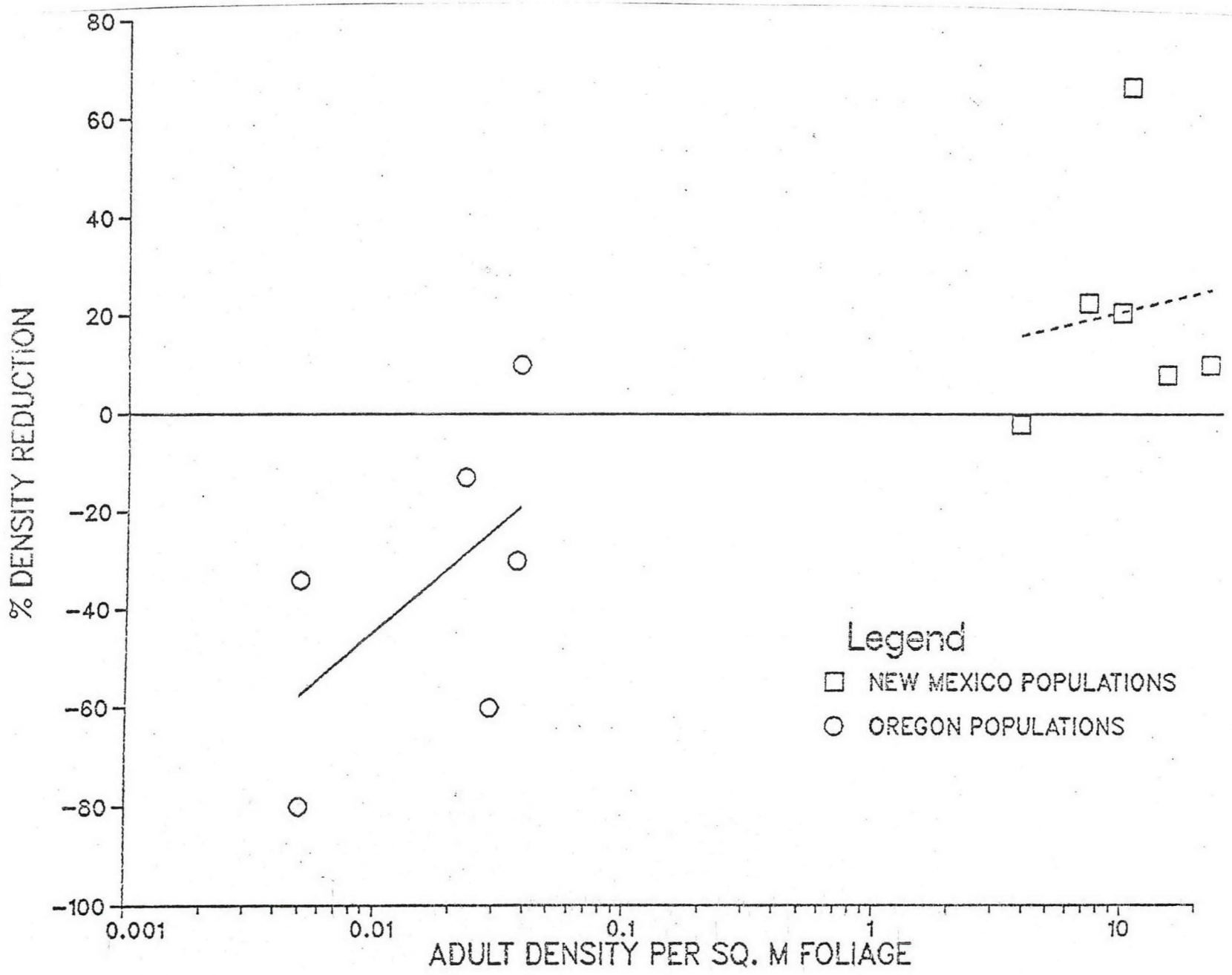
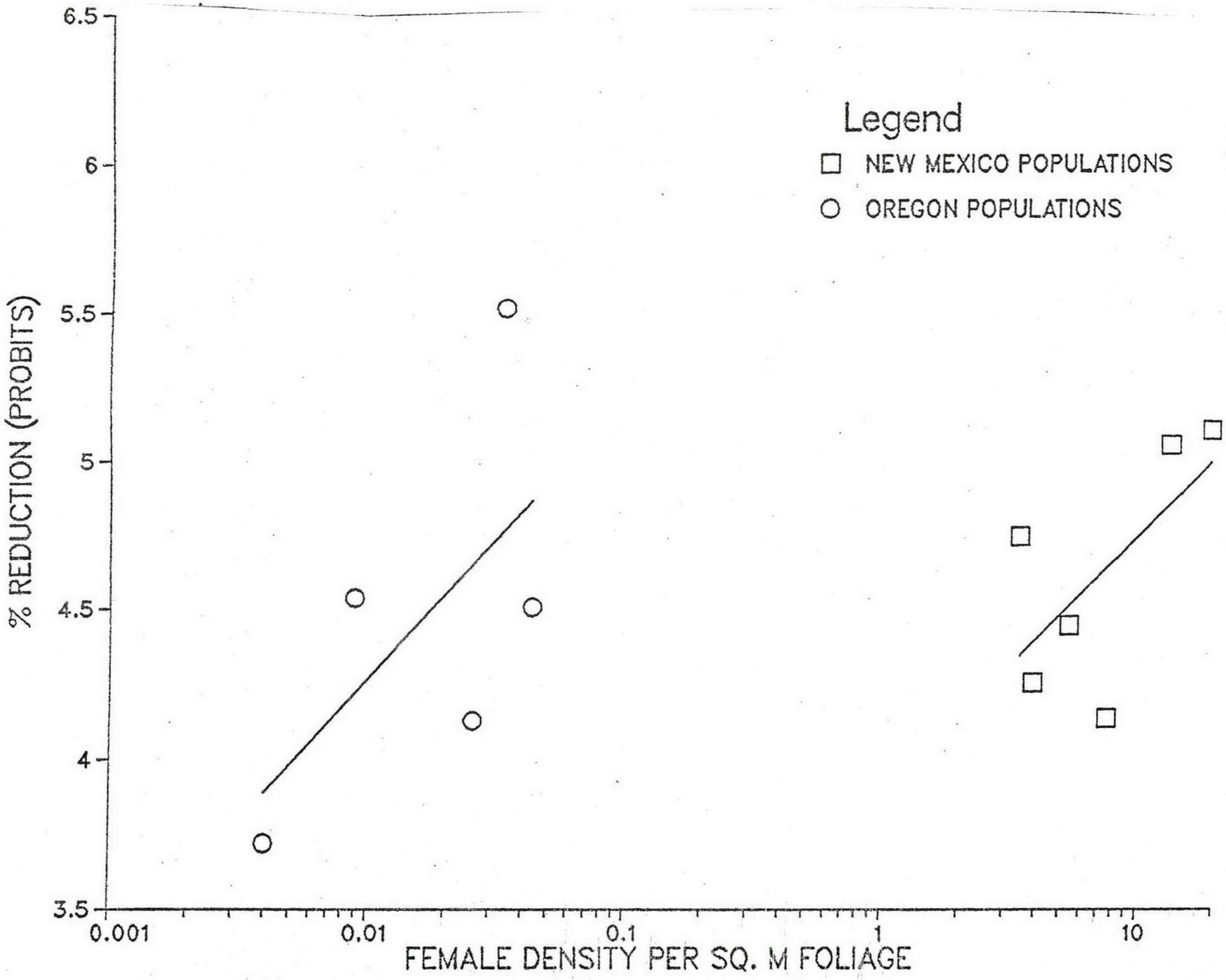

80
60
40
20
0
-20
-40
-60
-80
-100
% DENSITY REDUCTION
0.001
0.01
0.1
1
10
ADULT DENSITY PER SQ. M FOLIAGE
Legend
NEW MEXICO POPULATIONS
OREGON POPULATIONS

FIGURE 6


Legend
NEW MEXICO POPULATIONS
OREGON POPULATIONS
% REDUCTION (PROBITS)
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6
5.5
5
4.5
4
3.5
0.001
0.01
0.1
1
10
FEMALE DENSITY PER SQ. M FOLIAGE

FIGURE 7

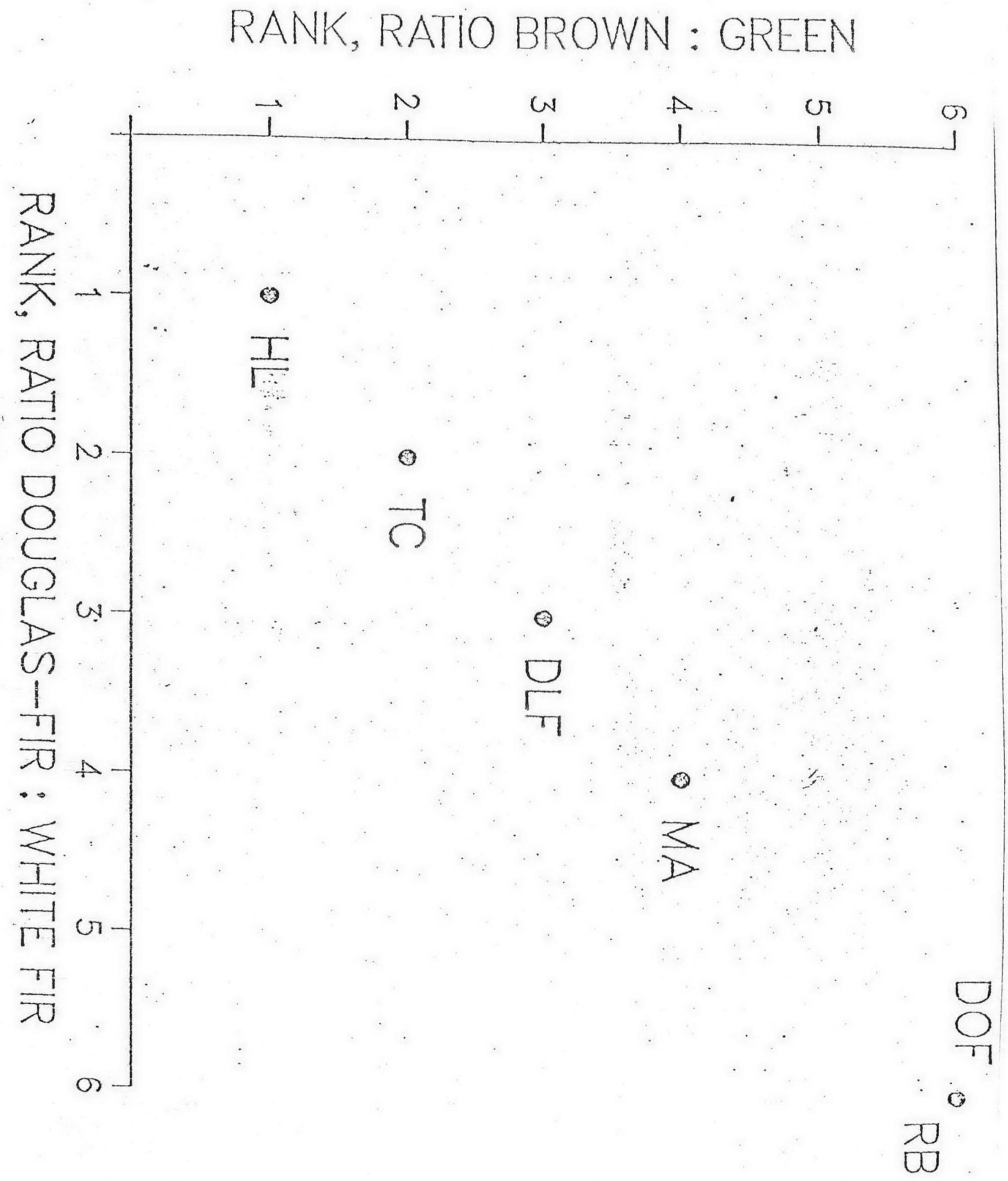

RANK, RATIO BROWN : GREEN
1
2
3
4
5
6
RANK, RATIO DOUGLAS-FIR : WHITE FIR
1
2
3
4
5
6
HL
TC
DLF
MA
DOF
RB

FIGURE 8

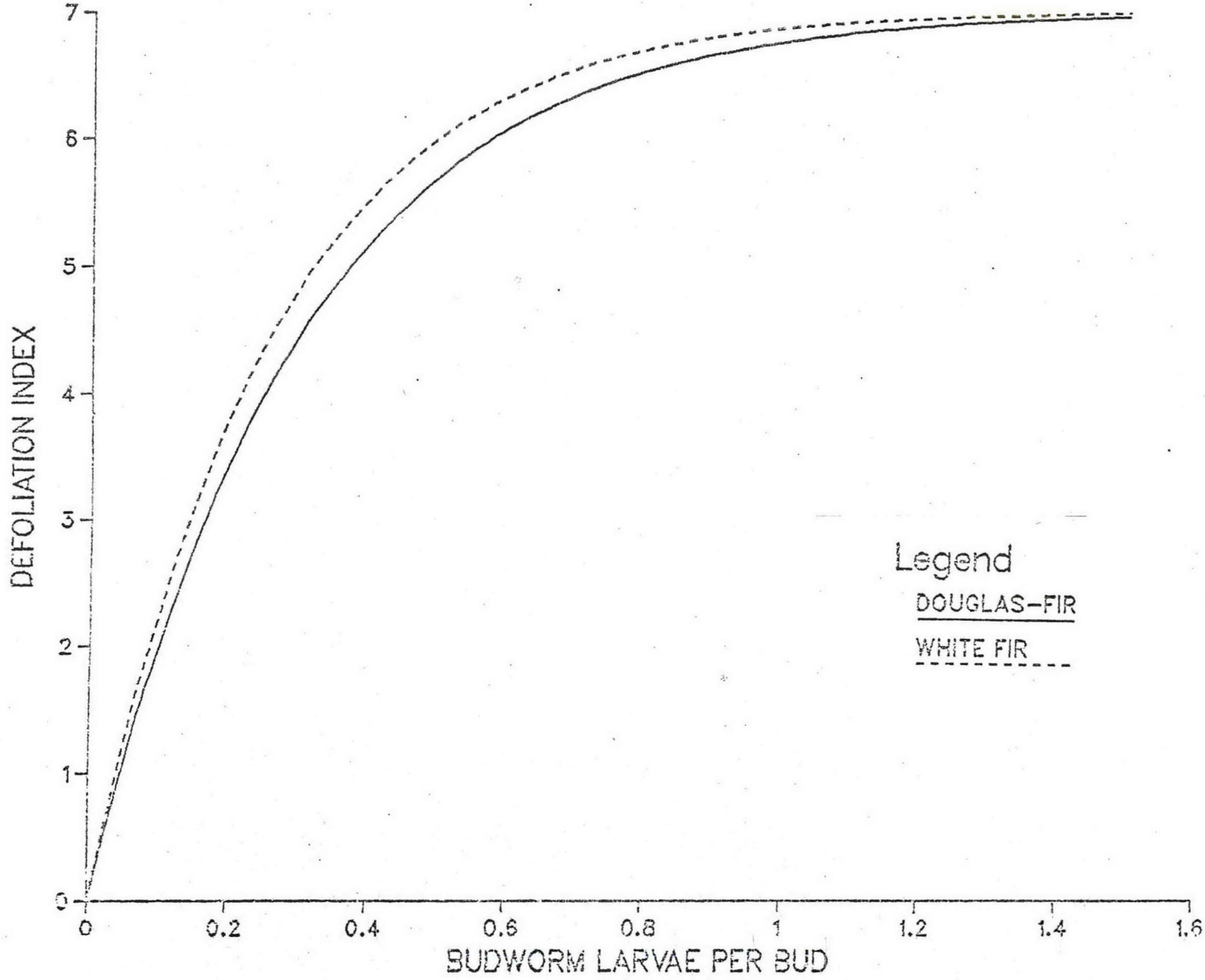

DEFOLIATION INDEX
0
1
2
3
4
5
6
7
0
0.2
0.4
0.6
0.8
1
1.2
1.4
1.6
BUDWORM LARVAE PER BUD
Legend
DOUGLAS-FIR
WHITE FIR

FIGURE 9

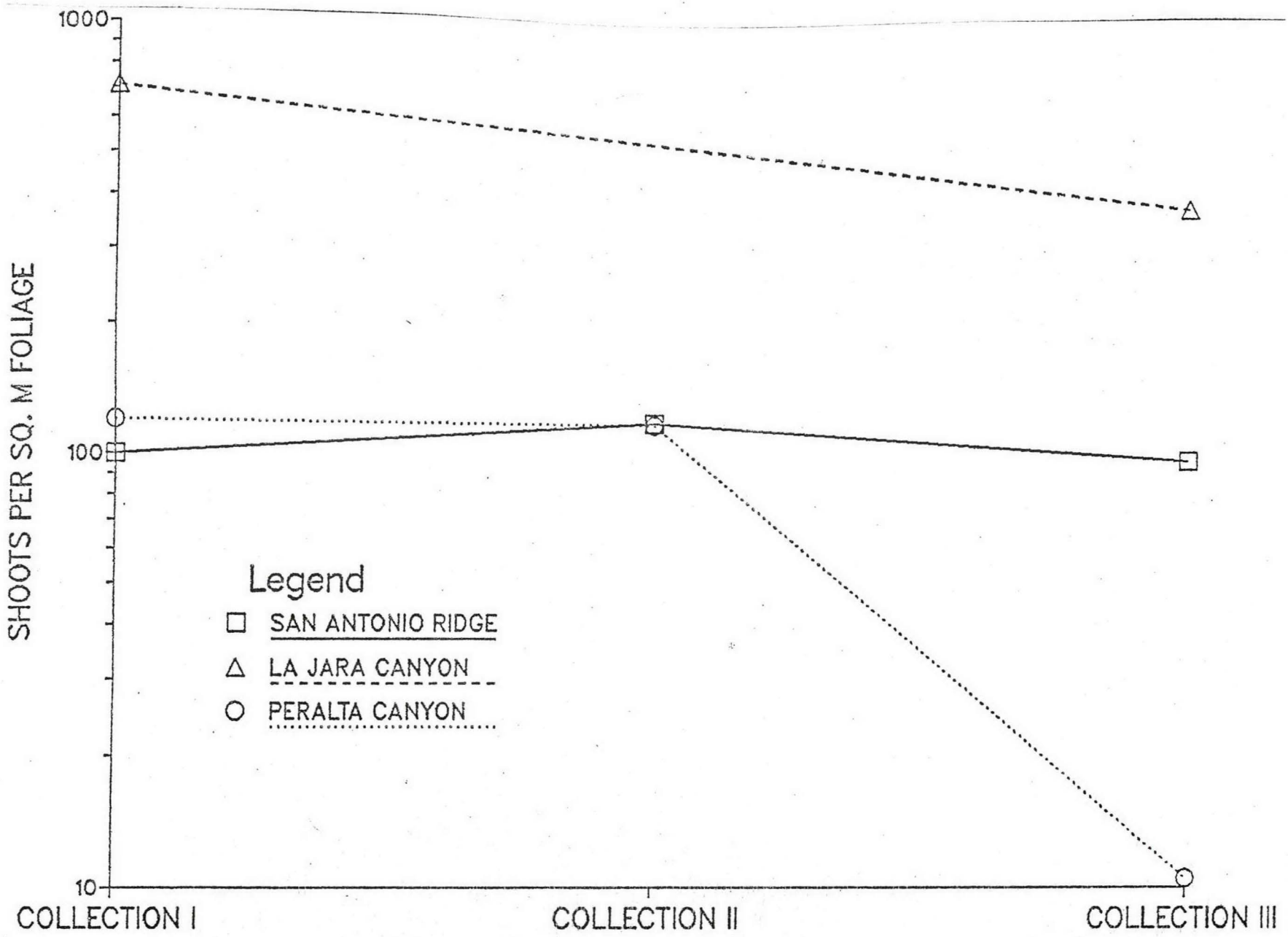
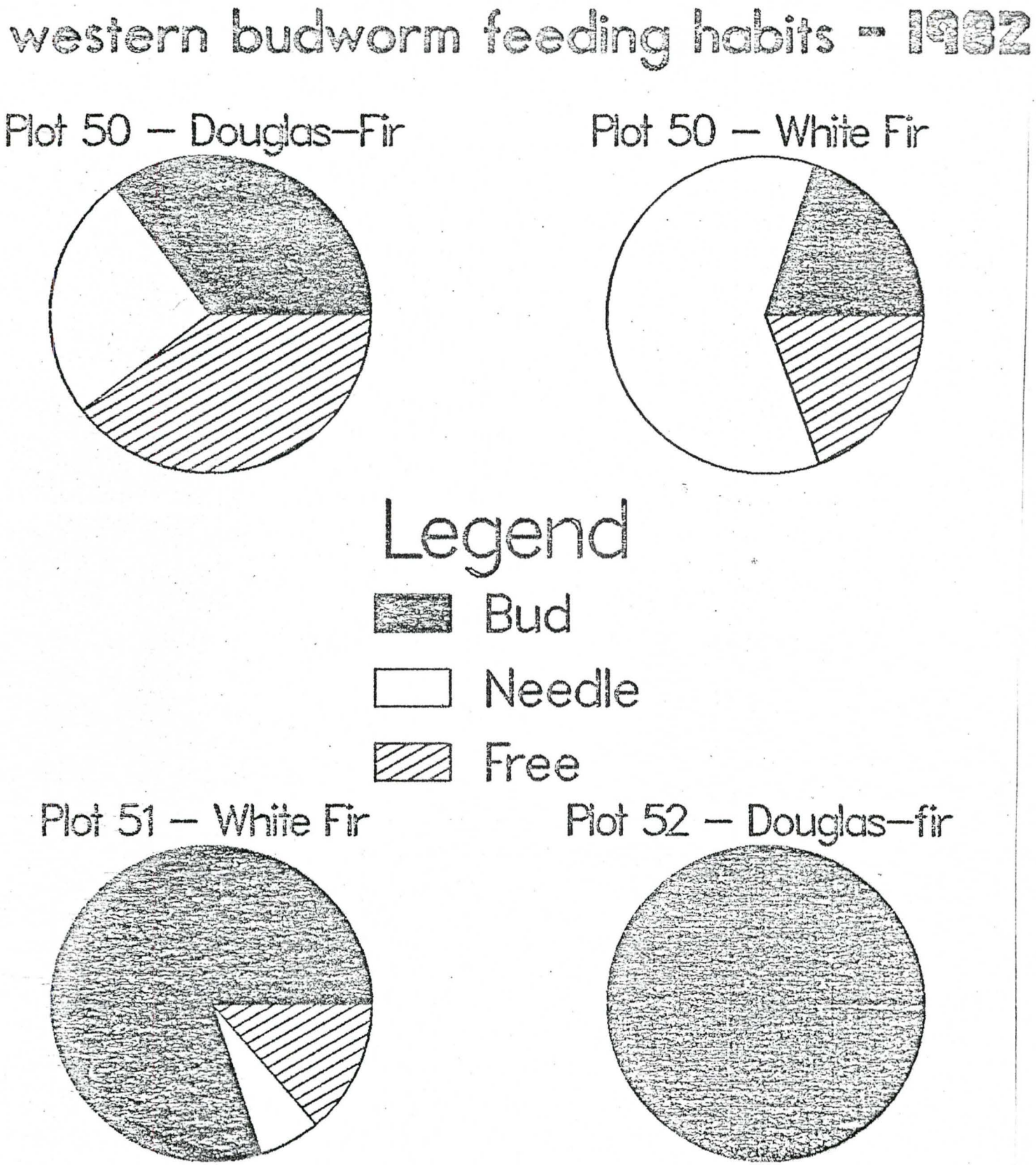

1000
100
10
SHOOTS PER SQ. M FOLIAGE
Legend
SAN ANTONIO RIDGE
LA JARA CANYON
PERALTA CANYON
COLLECTION I
COLLECTION II
COLLECTION III

FIGURE 10


western budworm feeding habits - 1982
Plot 50 – Douglas–Fir
Plot 50 – White Fir
Legend
Bud
Needle
Free
Plot 51 – White Fir
Plot 52 – Douglas–fir

APPENDIX

PUBLISHED PAPERS

Volney, W. J. A., W. E. Waters, R. P. Akers, and A. M. Liebhold 1983. Variation in spring emergence patterns in Choristoneura spp. populations in southern Oregon. Can. Ent. 115:199-209.

Volney, W. J. A., A. M. Liebhold and W. E. Waters. 1983b. Effects of temperature, sex, and genetic background on the coloration of Choristoneura populations in south-central Oregon. Can. Ent. 1583-1596.

MANUSCRIPTS IN PRESS

Liebhold, A. M. and W. J. A. Volney. 1983. Effect of foliage proximity on attraction of Choristoneura occidentalis and C. retiniana (Lepidoptera:Tortricidae) to pheromone sources. J. Chem. Ecol.

Liebhold, A. M., W. J. A. Volney and W. E. Waters. 1983. Evaluation of cross-attraction between sympatric Choristoneura occidentalis and C. retiniana (Lepidoptera : Tortricidae) populations in south central-Oregon. Can. Ent.

Volney, W. J. A., A. M. Liebhold and W. E. Waters. 1984. Host associations, phenotypic variation, ant mating compatibility of Choristoneura occidentalis and C. retiniana (Lepidoptera: Tortricidae). Can. Ent..

Waters. W. E. and W. J. A. Volney. 1984 Sampling and analysis of endemic western spruce budworm populations. In Site Characteristics and Population Dynamics of Lepidopteran and Hymenopteran Forest Pests. Brit. For. Comm.

MANUSCRIPT SUBMITTED FOR PUBLICATION

Liebhold, A. M. and Volney, W. J. A. 1983. Temporal factors affecting reproductive isolation between Choristoneura occidentalis and C. retiniana (Lepidoptera: Tortricidae). (Submitted to Can. Ent.)

MANUSCRIPTS IN PREPARATION

Liebhold, A. M. and W. J. A. Volney 1984. Specificity of male Choristoneura occidentalis and C. retiniana (Lepidoptera: Tortricidae) attraction to sex pheromone components.

Volney, W. J. A., A. M. Liebhold and W. E. Waters. 1984. Development rates of Choristoneura occidentalis and C. retiniana (Lepidoptera: Tortricidae), and their

hybrids.

Waters, W. E, Volney, W. J. A., and A. M. Liebhold. 1984. Spatial variation in density and survivorship of the western spruce budworm under endemic and epidemic conditions.